

Non-random patterns of spider species composition in an Atlantic rainforest

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Abstract. Spider species respond differently to variations in habitat structure; thus, differences in habitat structure may be responsible for variations in species composition of assemblages. However, little information exists on patterns of variation in spider species composition in tropical rainforests. We collected spiders and measured five different microhabitat characteristics in 20 sampling plots distributed among secondary and primary forest patches in an Atlantic rainforest, Brazil. Using multivariate analysis (non-metric multidimensional scaling - NMS), we checked for the existence of non-random patterns in the species composition of aerial (AG) and ground (GG) macroguilds, respectively. We also explored the relationships of those patterns with gradients in microhabitat characteristics and the influence of forest type (primary or secondary forest). We detected non-random patterns in spider species composition unrelated to microhabitat characteristics but differing between primary and secondary forest plots for both macroguilds. We discuss possible implications for studies of spider species composition and spider conservation in tropical forests.

Keywords: Araneae, community ecology, microhabitat gradients, guilds, conservation, tropical forests

Resumo. As espécies de aranhas respondem de modo distinto a variações na estrutura do habitat. Por esta razão, diferenças nestas estruturas poderiam ser responsáveis pela variação na composição de espécies das assembléias. Contudo, existe pouca informação a respeito de padrões na variação da composição das assembléias de aranhas em floresta tropical. Neste trabalho, foram coletadas aranhas e mensuradas cinco diferentes características de micro-habitat em 20 unidades amostrais distribuídas em áreas de floresta primária e secundária de floresta tropical Atlântica. Utilizando análises multivariadas (ordenação multidimensional não métrica - NMS), procurou-se a existência de padrões não aleatórios na composição de espécies de aranhas de macroguildas aéreas (AG) e de chão (GG), respectivamente. Investigou-se também, a relação destes padrões com gradientes nas características de micro-habitat e a influência do tipo de floresta (floresta primária e secundária). Foram detectados padrões não aleatórios na composição de espécies de aranhas, não relacionados às características de micro-habitat, todavia influenciados pelo tipo de floresta. Discute-se, portanto, a possível problemática de estudos que abordam composição e conservação de espécies de aranhas em florestas tropicais.

The knowledge of species composition patterns can be a useful tool for habitat management planning directed towards conservation (Primack & Rodrigues 2001). However, with the disturbance of the last remnants of the original habitat (Myers et al. 2000) we might lose the chance of rescuing the original patterns of local spider species distribution.

Spiders select different structures for living in their habitats (Robinson 1981; Greenstone 1984; Heikkinen & MacMahon 2004) and their populations respond to structural gradients in the habitat (Colebourn 1974; Lubin et al. 1993). Different characteristics of spider assemblages, like abundance of some groups, richness, or diversity, also change along gradients in vegetation density (Rypstra 1983, 1986; Balfour & Rypstra 1998; Gunnarsson 1988, 1990; Halaj et al. 1998). This is a result of the different responses of species exposed to the same gradients (Raizer & Amaral 2001; Wagner et al. 2003). In this way, gradients in vegetation structure might be responsible for gradients in species composition.

Most previous studies of tropical forest spider assemblages have compared richness estimators (Álvares et al. 2004; Sorensen 2004; Candiani et al. 2005; Indicatti et al. 2005; Oliveira-Alves et al. 2005; Dias et al. 2006; Nogueira et al. 2006), diversity and community structure indices between different rainforest fragments (Greenstone 1984; Russel-Smith & Stork 1994; Floren & Deeleman-Reinhold 2005; Barlow et al. 2007). Studies on assemblage composition in rainforest fragments have been limited to sunny regions of rainforests, such as canopies (Russel-Smith & Stork 1995) and clearings (Peres et al. 2007). Therefore, we know almost nothing about the patterns of variation in spider species composition in the shaded regions of rainforests.

Arachnid assemblages in primary forest fragments exhibit higher spatial species turnover when compared to secondary forests (Floren

& Deeleman-Reinhold 2005; Nogueira et al. 2006; Barlow et al. 2007; Bragagnolo et al. 2007). Primary forest fragments have usually been considered homogeneous in their conditions when compared to secondary fragments (Floren & Deeleman-Reinhold 2005; Nogueira et al. 2006; Barlow et al. 2007; Bragagnolo et al. 2007). However, the best preserved forest remnants consists of a mixture of secondary and primary forest, supporting the possibility of gradients in structural characteristics (as they function as microhabitats for spiders) to which the spatial species turnover might be related.

The exuberant diversity of arthropods in tropical areas requires a considerable effort for collecting, classifying, and analyzing local taxocenoses (Lawton et al. 1997). Höfer & Brescovit (2001) divided Neotropical spiders into guilds the members of which forage in the same microhabitats. Classifications like this allow us to separate the high levels of diversity present in tropical rainforests into ecologically recognizable and analytically treatable groups. Therefore, it becomes easier to associate gradients of species composition to gradients of microhabitat availability.

In this study, we looked for non-random patterns of spider composition in aerial and ground spider guilds in an Atlantic rainforest fragment in northeastern Brazil, and tested if they were related to gradients of microhabitat availability. We also tested if species composition and microhabitat gradients differ between primary and secondary forest fragments. Finally, as spider species inventories are scarce in this region of South America, we provide a list of species with abundance data as online material.

METHODS

Field work took place in the Fazenda Camuruji (12°30'5"S, 38°2'19"W), a private farm, owned by the Garcia D'Ávila foundation, and located in the in Açu da Torre village, Mata de São João district,

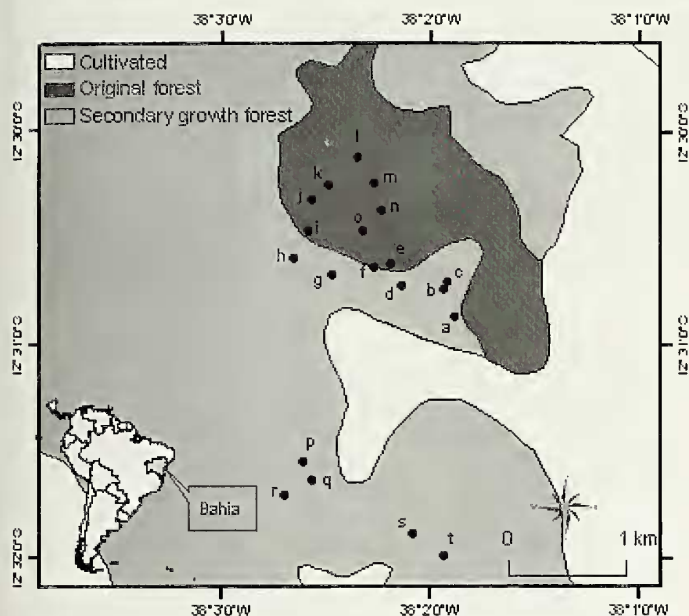


Figure 1.—Map of study area, with position of sampling plots among vegetation types, and location of study site inside the state of Bahia, northeastern Brazil.

100 km north to Salvador de Bahia, northeastern Brazil. This fragment contains 1,390 ha of ombrophylous lowland rainforest and presents a softly undulated geomorphology, typical for the region (Ab'saber 1977). A part of the forest was partially logged 35 years before but primary forest still exists. This fragment is one of the best preserved in the northern littoral of Bahia. This makes it critically important for conservation and study of the arachnofauna since significant forest patches are virtually nonexistent in Northeastern Brazil (Morellato and Haddad 2000). Mean temperatures in this region vary between 21°C and 26°C. Annual rainfall reaches 2000 mm, and rains are more concentrated from March to July (Instituto Nacional de Meteorologia. Online at <http://www.inmet.gov.br>).

Sampling design.—We sampled in 20 rectangular plots of 30 m × 5 m identified by letters (a, b, c, d...o; Fig. 1). Two complementary sampling methods were used: beating tray and hand collecting by visual searching. We used the beating-tray method to sample 15 bushes (all ≤ 3 m in height) of different species per plot, selected haphazardly. In each plot we invested an effort of two persons per hour in each expedition of active diurnal searches. We sampled each plot once in each of two five-day expeditions (January and March 2006). We distributed the plots systematically in the forest fragment. To do this, we walked 5 minutes along the main trails and then randomly chose the side of the trail and the distance from the plot to the trail (10 to 100 m). After a plot was established, we came back to the main trail and repeated the process. The forest fragment presented two forest types (data from the state's environmental resources council, Superintendência de Políticas Florestais, Conservação e Biodiversidade. Online at <http://www.meioambiente.ba.gov.br/>); thus we placed 12 plots in secondary forest (35 years old) and 8 in original primary forest (Fig. 1). The taxonomist, A.D. Brescovit, classified the specimens to species or morphospecies level. Specimens were deposited in the Butantan Institute's Collection (IBSP, curator A.D. Brescovit) and the Zoology Museum of the Federal University of Bahia (MZUFBA, curator T.K. Brazil).

Measurement of microhabitat availability.—In each plot we measured the availability of five different microhabitat characteristics. Leaf litter cover and grass cover were estimated according to Fournier's scale (Fournier 1974). We counted the number of fallen trunks with more than 15 cm in circumference and saplings with less

than 15 cm in circumference. We also measured the diameter at breast height of all trunks with more than 15 cm in circumference. All measurements were made within a 5 m radius around 4 points placed 10 m apart.

Analysis.—We deleted all singletons from the analysis, since their position in one plot does not give reliable information on their ecological requirements. We divided the species into two "macroguild" matrices, according to Höfer & Brescovit (2001). The first macroguild matrix (aerial macroguild, AG), included species belonging to guilds that forage at medium height in the understory such as nocturnal aerial runners (Anyphaenidae, Clubionidae, Mimetidae, Salticidae, Segestriidae), aerial ambushers Thomisidae), sedentary sheet weavers (Pholcidae and Pisauridae), aerial space web builders (Dictynidae and Theridiidae), aerial orb weavers (Araneidae, Tetragnathidae, Uloboridae, and Theridiosomatidae), nocturnal aerial ambushers (Senoculidae, Sparassidae, and Salticidae), and diurnal aerial hunters (Oxyopidae). The ground macroguild (GG) included species belonging to guilds that forage on the ground: diurnal ground runners (subfamilies Castianeirinae and Corinninae from Corinnidae), nocturnal ground weavers (Deinopidae and Dipluridae), diurnal ground weavers (Mysmenidae and Linyphiidae), ground ambushers (Idiopidae), and leaf litter stalkers (Miturgidae). The morphospecies belonging to Euophryinae (Salticidae), *Nothroctenus* Badcock 1932, *Celaetychaeus* Simon 1897 and *Ctenus* Walckenaer 1805 (Ctenidae) should belong to the aerial macroguild according to the classification proposed by Höfer & Brescovit (2001). However, our observations indicated that they forage on the leaf litter and thus we included them in the ground macroguild. A tree fell over plot "h" between the sampling trips; therefore we decided to remove it from the ordinations but maintained it in the total counts and the species list.

To detect non-random variation axes in species composition, we performed a non-metric multidimensional scaling (NMS) analysis on each macroguild matrix using PC-ORD[®] (see McCune & Grace (2002) for a comprehensive explanation of NMS method). NMS orders the plots on axes according to their similarity in species composition. In this way, the relative similarity in species composition among plots is represented by the differences between their axis scores. NMS does not assume linear relationships between species and environmental gradients. Because of that it is especially appropriate for reduction of species composition matrices, which seldom fulfil those assumptions. Our choices for performing the analysis followed recommendations from McCune & Grace (2002). First, we performed an exploratory analysis in the PC-ORD[®] program (McCune & Grace 2002) to detect the best options for representation of variation in species composition. We used the following choices: 6 possible dimensions, instability criterion of 0.005, 500 iterations, 999 runs with real data and 999 runs with randomized data. As the exploratory analysis indicated that one axis ordination was recommended, we represented the variation of each macroguild matrix on one axis. Abundances of each species in each plot were divided by the total of spider caught in each plot. Relative abundances were analyzed, the Bray Curtis coefficient was selected as the distance measure, and we used a random starting point and 500 runs with real data to find the best representation of the data on one axis (McCune & Grace 2002). We applied a Monte Carlo test, with 999 runs of randomized data, to test if our ordination was expected from a randomized version of the composition matrix. Our criterion for evaluating stability of the solution was standard deviation in stress equal to or less than 0.002, with 100 iterations to evaluate stability and 500 as the maximum number of iterations. Finally, the correlation of the distances between plots in the original abundance matrices with the distances in new ordered matrices was evaluated using a Mantel's test. We calculated the significance of the correlation via Monte Carlo randomization method with 999 randomizations.

We represented the main gradients in microhabitat descriptors across all the plots by performing a Principal Component Analysis

Table 1.—Descriptive statistics of microhabitats, measured in an Atlantic Rainforest fragment, northeastern Bahia. Abbreviations: DBH, diameter at breast height; GC, grass cover; LC, leaf litter cover; NS, number of saplings; NFT, number of fallen trunks.

	<i>n</i>	Range	Min.	Max.	Mean	S.D.
Grass cover (%)	19	55.0	25.0	80.0	57.1	16.9
Leaf litter cover (%)	19	15.0	85.0	100.0	96.6	5.3
Number of fallen trunks	19	19.8	4.0	23.8	13.1	6.1
Diameter at breast height (cm)	19	457.3	214.5	671.8	439.2	153.3
Number of saplings	19	24.8	7.6	32.4	18.0	5.9

(PCA), based on the correlation matrix and using varimax rotation (SPSS 12 for windows program). We tested the relationship between NMS and PCA axes via linear regression. To test the difference in species composition and microhabitats between primary and secondary forest plots, we first performed a Levene test to detect differences in composition variation (beta diversity), and a Welch *t*-test to detect differences in NMS and PCA scores (differences in species composition and microhabitat availability).

RESULTS

Sampling results.—From a total of 2082 collected spiders, 654 adult specimens were classified into 26 species and 104 morphospecies. The 130 species were distributed in 32 families. The four most abundant families were Salticidae with 32 species (24.2% of individuals), Pisauridae with only one species (13%), Theridiidae with 27 species (12.5%) and Thomisidae with 9 species (9.6%) (see online list at <http://www.redezoo.ufba.br/Specieslist.htm>). The most abundant and species rich guild was the nocturnal aerial runners with 741 specimens and 46 species. Sedentary sheet weavers was the second most abundant with 359 specimens. The second richest guild was the aerial space web builders with 27 species, followed by aerial orb weavers with 24 species. Two guilds, ground ambushers and leaf litter stalkers, were represented only by singletons, thus they were deleted from the analyses.

Gradients in species composition.—NMS detected a single non-random axis of variation for each of the two macroguilds (AG: 62 species, 15 families, Montecarlo $P = 0.004$, stress: 29.5%, instability: 0.025; GG: 9 species, 4 families, Montecarlo $P = 0.15$, stress 27.2%, instability: 0.015). The Mantel test showed that 66% of the original differences in species composition from AG and 73% from GG were explained by the NMS axes. Stress values close to 30% are high. However, stress depends on the number of species in the matrix (McCune & Grace 2002), which is very high when related to the number of plots (62 species in 20 plots) in the case of AG matrix. The instability criterion was also not met for the AG axis. This means that the ordination may give different results depending on the number of iterations. Due to this fact, we performed the ordination of the AG matrix several times and observed that the ordination of the non-random gradient in species composition was indeed constant, going from the plots a, b, c, d, o, to plots j, k, l, m.

Reduction of microhabitat descriptors.—PCA generated two axes (PCs) that represented a reasonable part of the total variation (74.5%) in microhabitat characteristics. The first axis (PC1: 44% of total variation), represented number of saplings (loading: 0.914), and leaf litter cover (loading: 0.871). The second axis (PC2: 30.5% of total variation) represented increasing diameter breast height of trees (loading: 0.758) and grass cover (loading: 0.689), and decreasing number of fallen trunks (loading: -0.729). A description of environmental variables is presented in Table 1.

The multiple regression analysis showed that none of the two PCs were significantly related to the species composition axes (AG: PC1: $b = 12016.14$; $P = 0.59$; PC2: $b = 4616.160$; $P = 0.83$; GG: PC1: $b = 9529.61$; $P = 0.72$, PC2: $b = 7086.47$; $P = 0.84$). This indicates that the microhabitat characteristics measured did not affect the species

composition gradients detected by the NMS analyses. Visually assessed normality of residuals did not deviate seriously from it.

Comparison of primary and secondary forest.—Despite the fact that the two macroguilds showed more variation in species composition in the primary forest (Mean \pm SD (range); AG: 0.31 ± 1.39 (-2.61 to 2.25); GG: 0.83 ± 0.93 (-0.80 to 2.16)) than in the secondary forest (AG: -0.13 ± 0.58 (-0.86 to 1.07); GG: -0.65 ± 0.40 (-1.36 to -0.07)), the differences were significant only for the AG NMS axis (Levene's test $P = 0.018$). Welch's *t*-test for unequal variances showed that primary and secondary forest types differed in species composition (NMS scores on the axis generated) only with respect to GG ($t = 4.377$, $df = 10$; standard error of difference 0.339; $P = 0.001$). Differences among PCA plot scores were not significant between primary and secondary forest plots (PC1: $t = 0.9236$, $df = 15$, standard error of difference = 0.467; $P = 0.3703$; PC2: $t = 0.4588$, $df = 16$, standard error of difference = 0.453; $P = 0.6525$). Thus, we found no gradients in microhabitat availability between primary and secondary forest plots that might explain the differences in species composition.

DISCUSSION

Both aerial and ground macroguilds showed one non-random axis of variation in species composition. Significant variations in species composition of tropical spider assemblages have been reported from comparisons between different fragments, usually related to different stages of ecological succession (Floren & Deeleman-Reinhold 2005; Nogueira et al. 2006) or when comparing *Eucalyptus* plantations with forest fragments in different stages of regeneration (Barlow et al. 2007). Nogueira et al. (2006) suggested that differences in vegetation structure between fragments in different forest stages of succession might determine the variation in spider species composition, since it is related to microhabitat diversity and microclimate conditions.

The availability of some microhabitats has been widely recognized as important for spider populations (Colebourn 1974; Lubin et al. 1993) and guilds (Rypstra 1983, 1986; Greenstone 1984; Balfour & Rypstra 1988; Gunnarsson 1988, 1990). In our study, however, variation in the availability of different vegetation attributes, such as grass cover, number of saplings, number of dead trunks and diameter at breast height, did not show any effect on spider species composition.

The extremely high spider species richness typical for tropical regions makes it difficult to detect a single variable that influences whole assemblages. However, we grouped the species sampled by similarity in microhabitat use (aerial and ground macroguilds) and then related the macroguilds to the main gradients in microhabitat availability (PC1 and PC2), representing several microhabitat descriptors at the same time. Theoretically, this should increase our ability to find an influence on species composition. As shown in Table 1, the ranges of variation in microhabitat availability were variable among the different descriptors. However, they might not have been enough to influence the relative abundance of an important number of spider species. Russel-Smith & Stork (1995) studied spider species composition along the canopy of a humid tropical forest in Borneo and did not find any influence of tree structural and taxonomic variation on species composition. Peres et al. (2007) found

differences in composition of spider assemblages in an Atlantic forest fragment when comparing natural treefall gaps with the surrounding forest. Additionally, they found significant differences in habitat structure and microclimate conditions. These results suggest that gradients of spider species composition in tropical forests might be related to strong variations in microclimate conditions, such as those related to treefall gaps, instead of variation in the availability of different physical structures or microhabitats. However, additional experimental studies on rainforest spiders' tolerance to perturbation in microhabitat availability should illuminate their sensibility to human made perturbations.

Another reason for not finding significant relationships between microhabitat availability and non-random changes in the composition of spider assemblages are that other, stronger, factors are affecting them. In our study, both axes of species composition were significantly affected by the stage of ecological succession of the patch: AG presented higher variation in species composition among plots from the primary forests, and species composition was significantly different for GG. Since only one patch of each stage of regeneration was available in the fragment, the samples are arguably non-independent because plots in the primary forest are neighbors in one part of the fragment (see Fig. 1). Despite the plots being geographically more dispersed in the secondary forest patch, none of the two macroguilds showed less variation in species composition inside the primary forest (in fact, AG showed significantly higher variation). This is contrary to what would be expected if distance was related to similarity in composition. Tropical forests are generally considered as homogeneous systems when they are compared (Floren & Deeleman-Reinhold 2005; Mathieu et al. 2005; Nogueira et al. 2006; Barlow et al. 2007; Bragagnolo et al. 2007). The significant differences found for both macroguilds and higher species composition variation of AG in primary forest indicate that the history of perturbation inside a tropical forest fragment may be an important generator of spatial variation in species composition. Since tropical forests could present a heterogeneous mix of successional stages, therefore affecting species composition, future authors should be cautious with the selection of sampling sites inside their considered "primary" forests. We found higher variation in species composition in primary forest, but this was only significant for AG. Our results for AG agree with Floren & Deeleman-Reinhold (2005), who found that spatial species turnover was highest in primary forest, compared to isolated forest fragments. This supports the idea that higher spatial turnover in spider species composition is related to better preserved tropical forests and suggests two possibilities: a) that ground spiders might recover the spatial variation in species composition faster; b) that ground spiders might be more tolerant to habitat changes than aerial spiders, maintaining similar levels of spatial variation in species composition in situations of habitat change.

In our study we did not find gradients of microhabitat availability to be influenced by forest type (primary and secondary), nor did we find a relationship between gradients in microhabitat availability and spider species composition. Probably other habitat characteristics than those we measured can better express the subtle variation between forest types inside the same fragment and might be generating the changes in species composition. The largest distance between plots was less than two kilometers and the forest extends continuously between the plots. However, primary and secondary patches exhibited significantly different species composition for GG and a significantly increased variation between plots in secondary forest for AG.

What could be preventing the restitution of composition and composition variability in those macroguilds of spiders after thirty five years of recovery? The low population density of most spider species in our study suggests a possible hypothesis, testable and relevant to conservation. This is that the low population densities of most spider species in tropical forests may make them bad re-colonizers. If low population density deters tropical forest spiders from long term

recolonization in adjacent patches of habitat, even with the highest investments and the best techniques in vegetation restoration, most spider species might be doomed to extinction in tropical forests. Density dependence tests in recolonization ability of spider species, controlling for microhabitat dependence, could shed light on this problem.

ACKNOWLEDGMENTS

We would like to thank Juliana Costa Piovesan, Myna Lizzie, Mariana Vila-Flor, Dary Rigueira, Lina Almeida, Milena Camardelli, João Anderson de Góes, and Cláudio José da Silva for helping during field work. Adriano Paiva, the biologist responsible for management of Garcia D'Ávila foundation's lands, for allowing this study there; Mariana Cayres, from the Regional Environmental Council, for creating the vegetation map; Dr. Antonio Brescovit, for spider identification; Silvanir Souza and Jaqueline Souza for help to provide a list of species as online material; Cristina Rheims and Thiago de Sá for help with the translation. This study was supported by grants (scientific initiation) from FAPESB 3367/2005.

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Manuscript received 14 December 2007, revised 28 July 2008.